

A comparison of genetic diversity in Nubian ibex (*Capra ibex nubiana*) and Alpine ibex (*Capra i. ibex*)

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Alpine ibex (*Capra i. ibex*) have shown a remarkable recovery in recent decades after almost becoming extinct in the last century (GRODINSKY and STÜWE 1987). The recovery was the result of an alpine-wide, though largely uncoordinated conservation effort, re-establishing ibex populations through reintroductions and translocations (STÜWE and NIEVERGELT 1991). Despite the dramatic increase in ibex population numbers and often strong population growth, little attention has been given to the relationships of reintroduction methodology (i.e. number of founders, sex ratio, and number of releases) and population genetic characteristics.

Maintenance of heterozygosity levels or minimization of loss of genetic variability has become a primary goal in the population management of vulnerable species (LANDE and BARROWCLOUGH 1987). Recent population surveys have shown that genetic variability in alpine ibex was low when compared to that in natural populations of other ungulate species (STÜWE and SCRIBNER 1989; RANDI et al. 1991). Genetic similarity among ibex populations was related to stocking history, probably as a result of genetic drift occurring during reestablishment of the populations (STÜWE et al. 1991). A detailed analysis of the effects of such management actions on the genetic diversity of the newly founded populations may aid the development of strategies for future reintroductions of locally extinct populations of ibex and other species. To determine whether low alpine ibex genetic diversity was a result of management actions or was a phenomenon reflecting species-wide evolutionary history, we compared alpine ibex with Nubian ibex (*Capra ibex nubiana*), using the same genetic methodology. The latter were chosen as a control because no unmanaged alpine ibex populations exist, and the Nubian ibex appears to be the taxa geographically and systematically closest related to alpine ibex. We chose a population in the Negev desert currently numbering about 400 individuals (ALKON and MAN 1988). Several Nubian ibex populations have suffered severe population reductions in the past (BAHARAV and MEIBOOM 1981; KRAUSMAN and SHAW 1986; HABIBI and GRAINGER 1990). However, there is no evidence that the Negev population has undergone the repetitive reductions in population size, and the intensive management actions alpine ibex experienced in recent times.

Blood was analyzed from 149 alpine ibex captured 1988 through 1990 in the four French populations Barge ($n = 22$), Champagny ($n = 10$), Encombe ($n = 14$), and Maurienne ($n = 37$), the three Swiss populations Saastal ($n = 29$), Jollital ($n = 5$), and Mont Pleureur ($n = 11$), and the Italian population Gran Paradiso ($n = 21$). An additional 39 blood samples were obtained from Nubian ibex, caught in 1988 in Avdat Canyon National Park and Zin Nature Reserve, near Sede Boquer, Israel. Blood samples were obtained from live animals immobilized with Xylazine-based tranquilizing drugs (STÜWE and SCRIBNER 1989).

Fourteen enzymes encoded at 15 loci were examined for polymorphisms using horizontal starch-gel electrophoresis (MANLOVE et al. 1976): albumin (ALB), phosphoglucomutase-3 (PGM-3; EC 2.7.5.1), hemoglobin (HB), glucose phosphate isomerase-1 (GPI-1; EC 5.3.1.9), creatine kinase-2 (CK-2; EC 2.7.3.3), glucose-6-phosphate (G-6-P; EC 1.1.1.49), malate dehydrogenase-1 (MDH-1; EC 1.1.1.37), 6-phosphogluconate dehydrogenase (PGD; EC 1.1.1.44), malic enzyme-1 (MOD-1; EC 1.1.1.40), purine nucleoside phosphorylase (NP; EC 1.6.2.2), lactate dehydrogenase-1 (LDH-1; EC 1.1.1.2), eurythacitic acid phosphatase (EAP), peptidase-B (PEP-B; leucyl glycyl glycine as substrate; EC 3.4.11) and indophenol oxidase-1,2 (IPO-1,2; EC 1.15.1.1). Initial sample treatment and analysis followed STÜWE and SCRIBNER (1989).

Differences in levels of multi-locus heterozygosity were tested using contingency chi-square analysis (SOKAL and ROHLF 1981).

The percentage of polymorphic loci (13.3 % and 20.0 %), mean number of alleles per locus (1.2 and 1.5), and average direct-count heterozygosity (0.048 and 0.087) were all lower in alpine than in Nubian ibex, respectively (Table). Differences in multi-locus heterozygosity were significant ($\chi^2 = 24.64$, $P < 0.001$, $df = 3$).

Direct-count estimates of average heterozygosity, mean number of alleles per locus, percent of polymorphic loci, and allele frequencies at seven variable loci in alpine and Nubian ibex

Locus	Alpine ibex	Nubian ibex	Locus	Alpine ibex	Nubian ibex	Locus	Alpine ibex	Nubian ibex
NP 118	0.000	0.026	MDH-2 70	0.000	0.013	PGD 90	0.003	0.205
NP 100	1.000	0.949	MDH-2 100	1.000	0.987	PGD 100	0.997	0.795
NP 82	0.000	0.026	LDH-1 88	0.510	1.000	Sample size	149	39
MOD-1 100	1.000	0.231	LDH-1 100	0.490	0.000	Avg. H	0.048	0.087
MOD-1 111	0.000	0.769	PEP-B 100	0.678	0.000	# of alleles	1.2	1.5
EAP 86	0.000	0.026	PEP-B 112	0.322	0.769	% polym.loci	13.3	20.0
EAP 100	1.000	0.974	PEP-B 136	0.000	0.231			

Locus designations are provided in the text.

Average ROGERS (1972) genetic distance between Nubian and alpine ibex was 0.106, far exceeding the genetic distance among alpine populations (mean: 0.021, range: 0.002–0.058). However, this relationship is based on few loci, and is primarily due to the presence of unique alleles and frequency differences. Allelic variation among the 149 alpine ibex was detected at three loci out of 15 loci analyzed; PGD, LDH-1 and PEB-B. Among 39 Nubian ibex, six loci were variable: NP, MOD-1, EAP, MDH-2, PEB-B, and PGD. Of the seven loci variable among both taxa, only one locus (LDH-1) was fixed in Nubian ibex as compared to four loci (NP, MOD-1, EAP, and MDH-2) fixed in alpine ibex (Table 1). In addition, the PGD 90 allele was present in only one individual in alpine ibex (frequency: 0.003) but was found at a much higher frequency in Nubian ibex (0.205), indicating progressing fixation among alpine ibex. The PEB-B 112 allele was found in both taxa, while the PEB-B 100 allele was found in alpine ibex and the PEB-B 136 allele was found in Nubian ibex only (Table).

Alpine and Nubian ibex are not sympatric and there are no fossil indications they ever were since the radiation of *Capra* in the third faunal zone of the Pleistocene. Their taxonomic status is controversial. Both are considered subspecies by many authors (see SCHALLER 1977 for review), although HEPTNER (1966), and HARTL et al. (1990) separate them as species. HARTL et al. (1990) calculated the genetic distance by biochemical comparison of one individual each of alpine ibex, Nubian ibex, markhor (*Capra falconeri*), and Bezoar goat. Of these four taxa only alpine and Nubian ibex had previously been

considered subspecies (SCHALLER 1977). However, HARTL et al. (1990) found the greatest genetic distance between just those two, and suggested that these taxa also be considered separate species.

Since the separation of alpine and Nubian ibex from their common ancestor, allelic variation could either have been lost (through drift or selection), or added (through mutation). This could have occurred either as a natural consequence of intrinsic population processes, or as a result of manipulative processes in either of the taxa. We believe genetic divergence between alpine and Nubian ibex should not be based solely on time since common ancestry as used in genetic distance calculations. Such calculations assume on homogeneity of evolutionary rates within independent lineages. However, the severe population manipulations experienced by alpine ibex since the 16th century (STÜWE and NIEVERGELT 1991) very likely contributed to the shifts in allele frequencies, the loss of alleles, and the significantly lower level of heterozygosity observed today. The low genetic diversity discussed for Alpine ibex populations (HARTL 1986; STÜWE and SCRIBNER 1989; RANDI et al. 1991) as well as the observed genetic distance between alpine and Nubian ibex may thus be due in part to stochastic effects associated with human intervention rather than deterministic processes alone.

It is difficult to assess the significance of the degree of genetic divergence between Nubian and Alpine ibex in the absence of molecular markers which exhibit alternative fixation, and in light of the strong influence of human manipulations. Without further genetic comparisons within the genus *Capra* our results do not warrant a classification of alpine ibex and Nubian ibex as separate species, and we therefore accept the systematic evaluation by SCHALLER (1977).

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